SPECIES DIVERSITY AND HABITAT COMPLEXITY: DOES VEGETATION ORGANIZE VERTEBRATE COMMUNITIES IN THE GREAT BASIN?

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ABSTRACT.—In this study, we have examined the effect of vegetation structure on the three major vertebrate taxa in Great Basin habitats of southwestern Utah. The effect of increasing vegetation heterogeneity, both horizontally and vertically, on the diversities of lizards, rodents, and postbreeding birds was investigated. We found no statistically significant relationship between diversity of all animal taxa and horizontal vegetation heterogeneity, although lizard diversity tended to decrease with increasing heterogeneity and rodent diversity tended to increase. Bird species diversity was positively correlated with vertical habitat heterogeneity. Abundances were highest for rodents in pinyon/juniper habitat and highest for lizards and birds in areas with the highest grass cover. Species richness was highest in sagebrush habitat for rodents but highest for lizards and birds in pinyon/juniper. Evenness values were relatively similar and high for birds and rodents and were relatively high for lizards in all habitats except for pinyon/juniper, which had an evenness value of 0.38. For rodents and lizards, abundance was significantly correlated with the index for horizontal habitat heterogeneity. After logarithmic transformation, abundance of lizards was positively correlated with increasing vegetation complexity. Combined abundance of lizards and rodents was also positively correlated with vegetation complexity. Rodent and lizard abundances, however, were affected by different aspects of the habitat. After logarithmic transformation, lizard abundances increased significantly with increasing grass cover, whereas rodent abundances increased significantly with increasing shrub cover.

Spatial heterogeneity, or simply the complexity of vegetation structure both horizontally and vertically, appears to predict species diversity in some instances, and many authors have felt that this is the primary factor causing differences in species diversity in communities (Pianka 1967, Rosenzweig and Winakur 1969, Karr 1971). MacArthur was the first to indicate that species diversity could be correlated with habitat diversity (MacArthur and MacArthur 1961, MacArthur et al. 1962). Others have found a similar trend of increasing animal diversity with increasing habitat complexity. This trend has been seen for birds (Karr 1971, Karr and Roth 1971, Tomoff 1974, Willson 1974, Lancaster and Rees 1979, Beedy 1981), lizards (Pianka 1966), rodents (Rosenzweig and Winakur 1969, Feldhamer 1979, Pizzimenti and De Salle 1981), and spiders (Hatley and MacMahon 1980).

By far the greatest amount of literature on this topic deals with the relationship between breeding bird communities and habitat complexity. This is the first study to consider (1) the relationship between vegetation complexity and postbreeding bird assemblages and (2) to consider more than one vertebrate class in an area. This allows us to ask several questions about species diversity and habitat complexity. Do postbreeding assemblages of birds conform to the pattern of increasing diversity with increasing habitat complexity seen for many breeding bird assemblages? Do diversities of several major taxa in the same habitats respond in the same way to vegetation structure? If measures of species diversity do not correlate with vegetation structure, are other measures of the relationship between a taxon and habitat more meaningful and predictive?

METHODS

Study Area

The study area is in the Escalante Desert of Utah, in the southeastern portion of the Great Basin (Fig. 1). We set up four 1,000 m transects in each of the five habitats that are the dominant vegetation types in this area. These habitats were uniform areas of pinyon/juniper, sagebrush, greasewood/shadscale, grassland, and an area we termed mixed shrub because it was a heterogeneous mix of small shrubs and grasses different from the other four habitats. These habitats generally followed an elevational gradient from approximately 1,550 to 1,785 m, with greasewood/

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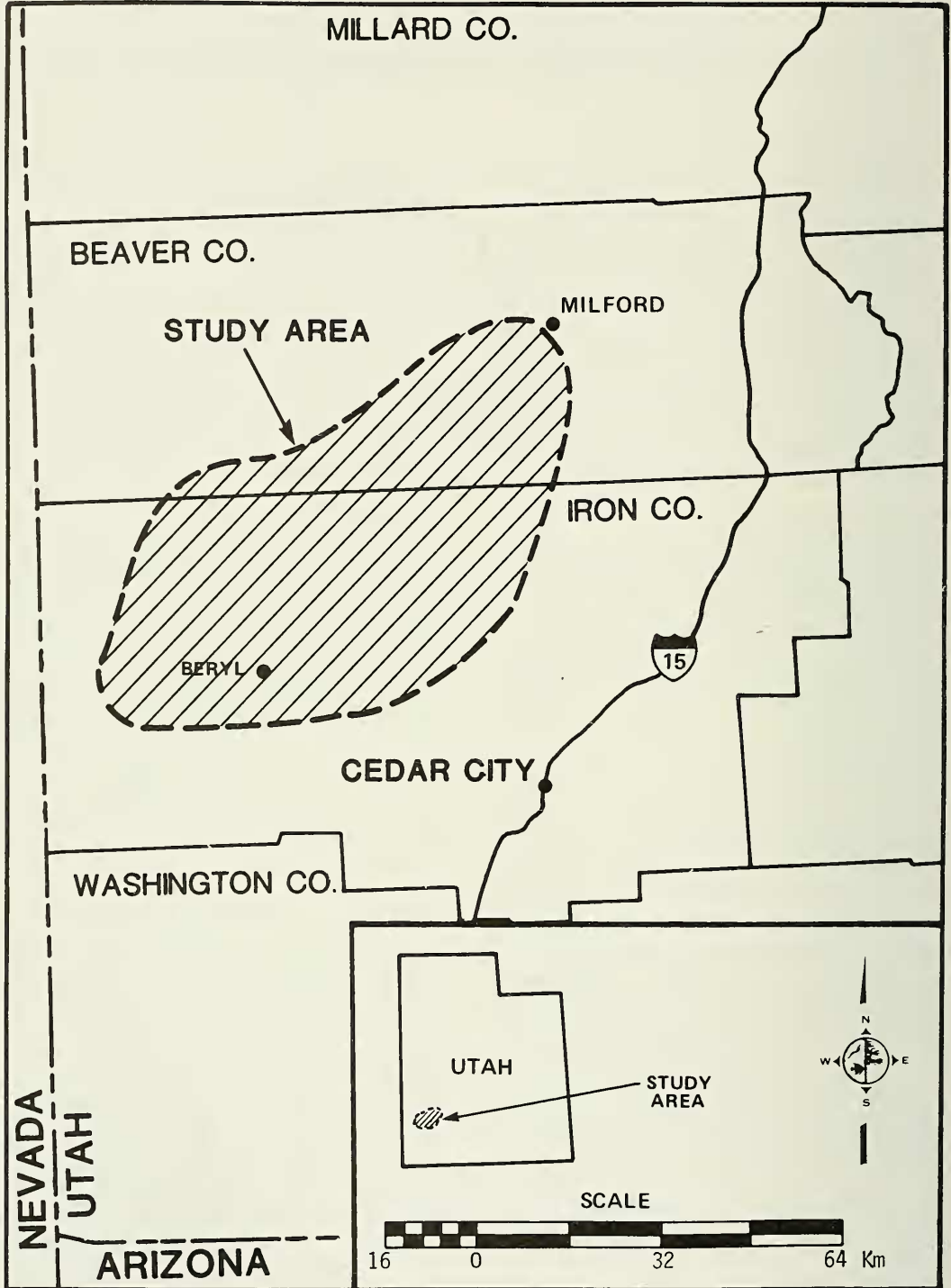
Fig. 1. The study site in southwestern Utah in the Escalante Desert. Four 1,000 m transects were established in each of five Great Basin habitats within the shaded area.

shadscale in the valley bottom and pinyon/juniper woodland on the foothills of the mountain range bordering this valley. The other habitats were at intermediate elevations. This area is characterized by hot summer temperatures and cold winters. Annual rainfall averages approximately 200 mm, with precipitation falling in all months. The highest amount of precipitation falls in March and April, approximately 50 mm, 23% of the total. Each of the other months averages about 15 mm of precipitation, approximately 7% of total.

Field Methods

Five experienced investigators carried out censuses of rodents, lizards, and birds in July and August 1981. We used visual walking censuses to determine the densities of lizards and birds. We censused birds between 0530 and 0800 and lizards between 0900 and 1200. We recorded the species and number of animals sighted, distance of each observation from the transect line, and the compass direction of each observation. This information was entered into a computer program (Burnham et al. 1980) that gave a density estimate for each species. This method of line-transect sampling takes into account differential visibility of individual animals in different habitats. Where cover is more dense, the effective distance of sighting a bird or lizard is reduced. This, in turn, reduces the width of the area censused on either side of the transect line. A smaller belt of area on either side of the transect line gives a smaller area sampled for the number of observations and therefore corrects for decreased visibility. This computer program generates a different size of area censused for each species and for each habitat. Density estimates were, therefore, determined with visibility being an integral part of that estimate.

Rodents were live-trapped at night using the assessment line technique (O'Farrell et al. 1977) to determine rodent density. This technique also includes the movement behavior of the animal at the time of censusing in making density estimates. The assessment lines are trapping stations located perpendicular to the two main parallel lines of trapping stations. The assessment lines give a maximum boundary around the main census lines for each species by recording the farthest distance individuals of a species are caught from the main census lines. The length of the main census lines multiplied by the width, as determined by trapping on the assessment lines, gives an estimate of the area censused for each species.

Vegetation sampling was done using the Daubenmire Nested Quadrat method (Mueller-Dombois and Ellenberg 1974) on the same transects used to census animals. Sampling yielded plant species abundance, percent density, and percent cover.

Data Analysis

Species diversity and evenness values were calculated from the richness and abundance data using indices from Hill (1973). These indices define diversity as $N_2 = 1/\Sigma(p_i^2)$, where p_i is the relative abundance of the ith species, and evenness as N_2/N_1, with $N_1 = \exp(-\Sigma p_i \ln p_i)$. The diversity index ($N_2$) expresses diversity with "species" as the basic unit and still includes an evenness component of species abundance pattern as well as richness. The diversity value calculated by this index is influenced more by the number and abundance of common species than rare species, although both are included in determining a diversity value. Hill (1973) points out that N_2 allows a more straightforward comparison among communities with different diversities and sample sizes (see Rotenberry 1978 for a summary of the advantages of using N_2 as a diversity index).

For vegetation we calculated indices for both horizontal and vertical heterogeneity. We determined horizontal heterogeneity using a habitat physiognomic complexity index (PCI) for each habitat type similar to that of Tomoff (1974). We determined this diversity index for each habitat again using the index N_2, where p_i equals the proportional cover value of each physiognomic component in the habitat (i.e., grass, cacti, forbs, shrubs, and trees). A habitat with only one or two of these components composing the majority of cover, or being the only components in the habitat, is not likely to have as much horizontal heterogeneity as a habitat that contains a somewhat equal mixture of components. We determined vertical heterogeneity using the Shannon-Weaver Information index, $H^2 = -\Sigma p_i \ln p_i$, to give foliage height diversity (FHD) where p_i is the proportion of the total cover of the foliage that lies in the ith vertical layer

TABLE 1. Cover values (percent total cover) of physiognomic components and diversity indices for each habitat type. Habitats are listed in order of elevation from lowest to highest.

Habitat	Physiognomic component					Diversity index	
	Forb	Grass	Cactus	Shrub	Tree	PCI	FHD
Greasewood/ Shadscale	0.01	0.04	0	28.18	0	1.00	0.06
Mixed shrub	0.28	14.62	0.08	17.08	0	2.03	0
Grassland	0.48	14.06	0	12.97	0	2.07	0
Sagebrush	0.03	5.34	0.21	22.49	0	1.47	0.50
Pinyon/Juniper	0.31	1.12	0.02	3.95	22.02	1.50	0.61

TABLE 2. Species richness, abundance (number per hectare), evenness, and diversity of the three taxa for a gradient of habitats. The habitat types are listed in the order of their PCI value from highest to lowest. PCI values for each habitat are listed in parentheses below the habitat type.

Taxon	Habitat Type				
	Grassland (2.07)	Mixed shrub (2.03)	Pinyon/ Juniper (1.50)	Sagebrush (1.47)	Greasewood/ Shadscale (1.00)
LIZARDS					
Species richness	5	2	7	5	3
Abundance	27.87	22.12	4.25	8.69	4.43
Evenness	.69	.94	.38	.75	.86
Diversity	2.02	1.03	2.21	3.05	2.77
RODENTS					
Species richness	6	5	5	9	5
Abundance	2.66	6.22	18.32	8.01	11.36
Evenness	.84	.93	.96	.74	.72
Diversity	3.24	2.50	2.80	2.62	2.04
BIRDS					
Species richness	3	6	25	6	7
Abundance	8.96	1.95	3.19	0.22	1.21
Evenness	.94	.85	.70	1.00	.83
Diversity	1.92	3.39	8.67	4.79	3.21

(MacArthur and MacArthur 1961). Vegetation was divided into layers of 0 to 0.5 m, 0.5 to 1.0 m, and > 1.0 m. We used correlation and regression statistics to find relationships between PCI, FHD, and animal diversity.

RESULTS

Values of PCI for each habitat type were highest in the two habitats with abundant grass cover and lowest in the greasewood/ shadscale, where virtually all the cover was composed of similar-height shrubs (Table 1). The grassland and mixed shrub habitats had highest PCI values by virtue of having an even mix of two physiognomic components, whereas the other three habitats were dominated by only one physiognomic component. The pinyon/juniper habitat contained all five vegetation components, but only the tree cat-

egory gave a significant cover value. Cover densities of forbs and cacti were low in all five habitats. Trees were present only in the pinyon/juniper habitat. However, values of FHD gave a different trend. The grassland and mixed shrub habitats, which gave the highest values for PCI, had values of 0 for FHD. Not too surprisingly, the highest value for FHD was for pinyon/juniper habitat.

For each animal taxon, the highest diversity indices occurred in different habitat types (Table 2). Birds showed the widest range in diversity values, with a high of 8.67 in pinyon/ juniper habitat and a low of 1.92 in grassland habitat. Diversities of rodents were the most similar, with a range of 2.04 to 3.24. Species richness was highest in the pinyon/ juniper for lizards and birds, but highest in the sagebrush for rodents. Birds also showed the widest range in species richness, with val-
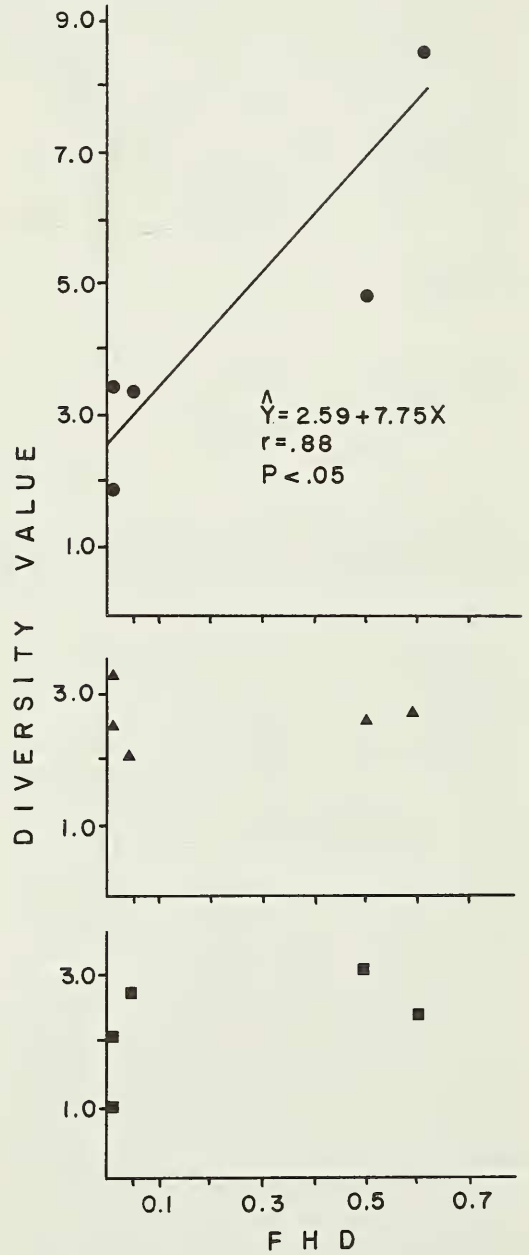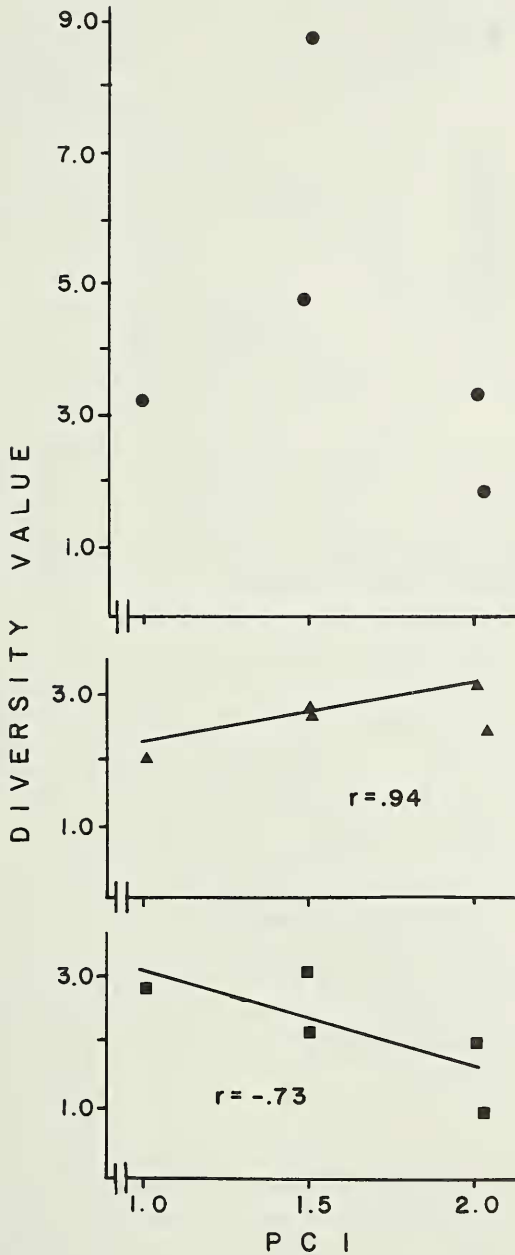
Fig. 2. Diversity values for birds (circles), rodents (triangles), and lizards (squares) versus the physiognomic complexity index (PCI) for five Great Basin habitats. Although the regression lines are not significant at the 0.05 level, trends are evident for lizards and rodents.

Fig. 3. Diversity values for birds (circles), rodents (triangles), and lizards (squares) versus foliage height diversity (FHD) for five Great Basin habitats. Lizards and rodents are not correlated to FHD, but postbreeding birds are significantly correlated.

ues from 3 to 25. Abundances were highest in the pinyon/juniper for rodents, but for birds and lizards they were highest in areas with abundant grass cover (Table 2, Appendices A, B, C). Although there is not a clear pattern,

the areas with the lowest species richness produced the highest, or nearly the highest, abundance for each taxon. Evenness values were relatively high for birds and rodents in all habitats, ranging from 0.70 to 1.00 for birds
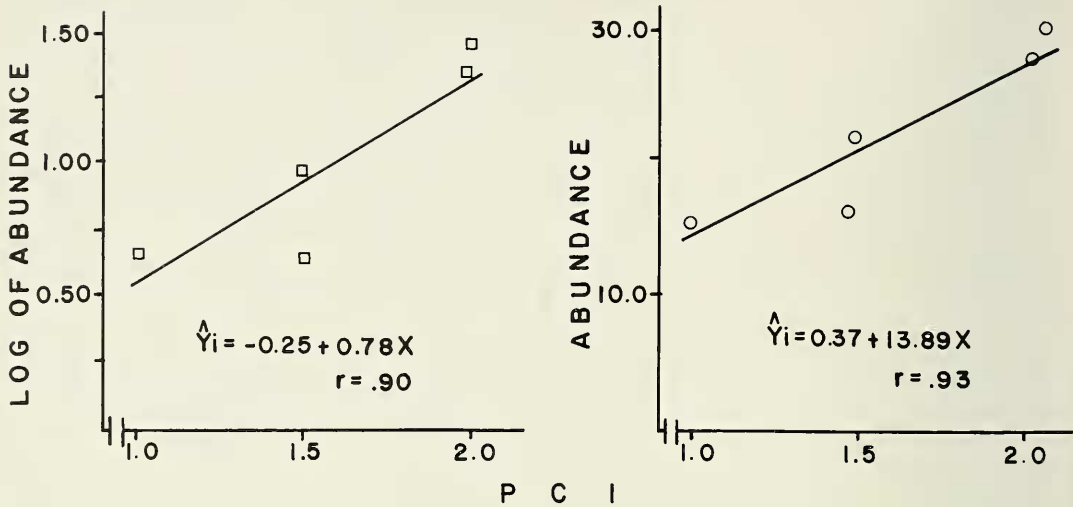
Fig. 4. The logarithmic transformation of lizard abundance (number per hectare) versus the physiognomic complexity index (PCI) for five Great Basin habitats on the left and the combined abundance (number per hectare) of rodents and lizards versus PCI for the same habitats on the right. Both regression lines are significant.

and 0.72 to 0.96 for rodents. For lizards, an unusually low evenness value of 0.38 was obtained for the pinyon/juniper habitat.

No statistically significant relationships came from plotting diversity indices for each taxon against PCI values for the five habitat types (Fig. 2), although rodent diversity was highly correlated to PCI and tended to increase with increasing PCI, and lizard diversity tended to decrease with increasing PCI. Bird diversity was positively correlated to FHD; lizard and rodent diversities were uncorrelated (Fig. 3). Although the relationships of diversity to horizontal habitat heterogeneity for rodents and lizards are suggestive, neither is statistically significant and therefore not wholly satisfying. We did find, however, that a component of diversity, abundance, was related to PCI in some instances. For lizards the logarithmic regression of abundance to PCI was significant and highly correlated, as was the regression of combined abundance for rodents and reptiles plotted against PCI (Fig. 4).

We looked at the above relationship more closely and found that lizard abundance increased with increasing grass cover. There is a significant (P < .05) negative relationship between percent grass cover and percent shrub and tree cover (r = −.96). As grass cover increased, there was a linear decline in overstory cover. Reptile abundance plotted against the ratio of percent grass cover over the percent shrub and tree cover gave a significant (P < .01) logarithmic relationship (r = .98, Fig. 5). As grass cover increased and overstory cover dropped, reptile abundance increased. We also found a significant (P < .05) inverse relationship between the logarithmic transformation of rodent abundance and the grass/overstory ratio (r = −.91 Fig. 5.) Rodent abundance decreased with increasing grass cover and increased with increasing shrub and tree cover. No pattern existed for bird abundances when plotted against the ratio of percent grass cover to percent shrub and tree cover.

DISCUSSION

In this part of the Great Basin, both lizard and rodent assemblages seem to be structured, at least in part, by the horizontal heterogeneity of the vegetation. Postbreeding bird assemblages are correlated with vertical heterogeneity.

For lizards there was a trend of decreasing diversity with increasing vegetation complexity. This trend is in contrast to the positive relationship Pianka (1966) found between the number of lizard species and plant volume diversity. Comparisons with this study are weak, however, because Pianka used species richness as his measure of animal diversity,
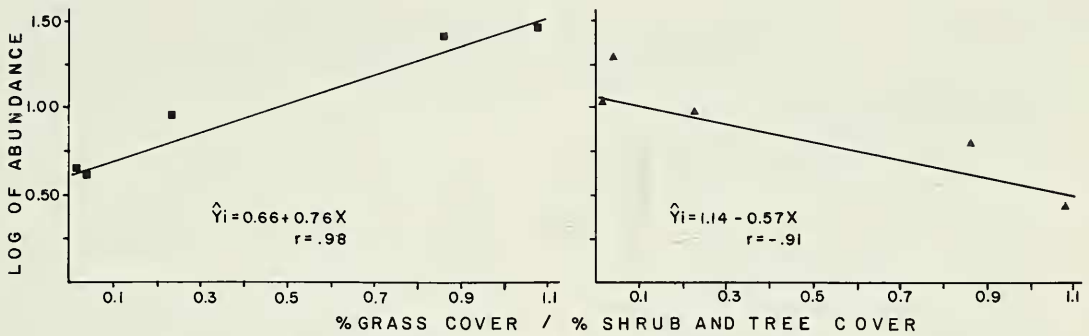
Fig. 5. The logarithmic transformation of lizard (squares) and rodent (triangles) abundances (number per hectare) versus the ratio of grass cover to shrub and tree cover in the five habitat types. Both regression lines are significant.

ignoring the abundance of each species. It should be noted that his vegetation complexity index is different from ours. The differences in these results may simply reflect the different indices used, although the number of lizard species we found in each habitat also did not correlate with vegetation complexity. We found that the abundance of lizards was significantly correlated with vegetation complexity and was positively correlated with an increasing percentage of grass cover in each habitat. This diverges from earlier findings by Germano and Hungerford (1981) in Sonoran desert grasslands, where relative abundance of reptiles was lowest in the area with the highest grass cover. Werschkul (1982), working in Great Basin habitat of Oregon, did not find any lizards in grassland habitat. Four of the five habitats we studied were numerically dominated by *Uta stansburiana*. In the two habitats with the highest lizard abundance, grassland and mixed shrub, *U. stansburiana* accounted for 68% and 98% of lizard abundance, respectively (Appendix A). In other areas that have been studied, *U. stansburiana* was not abundant in habitats with high grass cover (Fox 1978, Tinkle 1967, Werschkul 1982). Why was *U. stansburiana* most abundant in habitats with denser grass growth in the Escalante Desert? Fox (1982) found that juvenile *U. stansburiana* had better survival rates in habitats that are the most complex. In the area Fox studied, habitats that contained high grass cover were less complex, and this may be the general case in most areas; however, this is not the case in the Escalante Desert. Populations of *U. stansburiana* in the Escalante Desert may do better in these more horizontally heterogeneous habitats even

though these habitats have the highest grass cover.

Rodents followed the opposite trend: diversity increased with increasing vegetation complexity. This general pattern was reported for rodents in the Sonoran Desert (Rosenzweig and Winakur 1969). Rodent abundance was also significantly correlated with increasing cover of shrubs and decreasing cover of grass. Pizzimenti and De Salle (1981) found that abundance of insectivorous rodents in Peru is positively correlated with increasing plant cover. They did not discuss the composition of plant communities, so it is not known if grass or shrubs were increasing the most in these areas. Much of the abundance of the overall rodent communities in our study was due to the abundances of species of *Peromyscus* and *Perognathus*. These species were found to be closely associated with shrubby vegetation (Rosenzweig and Winakur 1969) but, as Parmenter and MacMahon (1983) found, such vegetation may not be entirely necessary. When they experimentally removed shrubs from a plot in southwestern Wyoming, they found no change in population sizes, sex ratios, or age structure for several rodent species, including *Peromyscus maniculatus* and *Perognathus parvus*, both of which were found at our site.

Combining abundance of rodents and lizards gave us a significant positive relationship with horizontal habitat heterogeneity. It appears that horizontal heterogeneity benefits both lizards and rodents by increasing their collective abundance in a way seen for lizard abundance and habitat complexity but not seen for rodents when rodent abundance is considered alone. We do not know of a

biological reason for this relationship in view of the fact that each taxon appears to occupy a different trophic level and each is separated in the habitat temporally.

Postbreeding bird diversity did not corre- late with horizontal habitat heterogeneity (PCI) but did correlate with vertical habitat diversity (FHD) in our study area. The lack of correlation between horizontal vegetation complexity and either bird diversity or abun- dance was similar to the work by Wiens (1973, 1974a, 1974b) in western shrubsteppe habi- tats where no correlation between bird diver- sity and vegetation complexity could be found. Postbreeding bird assemblages in our study area did correlate with vertical layering, which was similar to the relationship seen for breeding bird assemblages in both tropical and temperate locales (MacArthur and MacArthur 1961, Karr 1971, Willson 1974, Lancaster and Rees 1979, Beedy 1981). This relationship appeared to hold wherever there was a significant range of vertical layering. It is not surprising, therefore, that the highest bird diversity was found in pinyon/juniper habitat, the only habitat with trees. Willson (1974) has previously indicated that adding trees in a vegetation series is important to increasing bird species diversity. We also found highest bird abundances in areas with highest grass cover, which is similar to the pattern of bird abundances in other grassland situations (Rotenberry and Wiens 1980, Wiens and Rotenberry 1981).

The three major vertebrate taxa in this area appear to be structured differently in the same habitats. Postbreeding bird diversity is significantly correlated with vertical layering, but rodent and lizard diversities are corre- lated with horizontal habitat heterogeneity. These relationships could be expected given the plane of space in which these three taxa function. Many birds forage, nest, and roost in trees and therefore make greater use of verti- cal space than rodents or lizards. Rodents and lizards, on the other hand, are restricted more often to a horizontal plane of movement. If vegetation does structure rodent and lizard assemblages to some degree, then horizontal heterogeneity would likely act more strongly on their diversities, as this study has demon- strated. Statistically significant patterns for rodents and lizards appear only when the abundance of these taxa are considered.

Abundances of lizards and rodents are closely correlated with the percent of grass and shrub cover in the five Great Basin habitats we stud- ied.

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APPENDIX

Table A. Reptile density (number per hectare), by habitat type, in Great Basin habitats of the Escalante Desert, Utah.

Species	Habitat type				
	Pinyon/ Juniper	Sagebrush	Grassland	Mixed shrub	Greasewood/ Shadscale
Crotaphytus insularis	0	0.35	0	0	0
Gambelia wislizenii	0.50	1.04	3.80	0	0
Sceloporus occidentalis	0.25	0	0	0	0
S. graciosus	0	0.35	0	0	2.22
Uta stansburiana	1.75	4.52	19.01	21.74	1.33
Phrynosoma platyrhinos	0.25	0	1.90	0	0
P. douglassi	0.25	0	0.63	0.38	0.44
Cnemidophorus tigris	0.75	1.04	0.63	0	0
Unidentified lizard	0.25	1.39	1.93	0	0.44
Masticophus taeniatus	0.25	0	0	0	0
Species richness	7	5	5	2	3
Abundance	4.25	8.69	27.87	22.12	4.43

Table B. Rodent density (number per hectare), by habitat type, in Great Basin habitats of the Escalante Desert, Utah.

Species	Habitat type				
	Pinyon/ Juniper	Sagebrush	Grassland	Mixed shrub	Greasewood/ Shadscale
Dipodomys microps	0	0	0	0	1.02
D. ordii	0	0	0.01	0	1.53
D. sp.	0	0.01	0	0	0
Perognathus formosus	0.71	0	0.41	2.69	0
P. parvus	0	0.85	0	0.76	0
P. longimembris	0	0.01	1.19	2.77	0

Table B continued.

	Habitat type				
Species	Pinyon/ Juniper	Sagebrush	Grassland	Mixed shrub	Greasewood/ Shadscale
Microdipodops megacephalus	0	1.36	0	0	0
Peromyscus maniculatus	7.24	4.57	0.58	0.01	7.70
P. truei	7.98	0.96	0.01	0	0
P. boylii	0	0.01	0	0	0
P. eremicus	0	0	0	0	0.63
Onychomys leucogaster	0	0.27	0.48	0	0.48
Eutamias dorsalis	1.60	0	0	0	0
Neotoma lepida	0.79	0	0	0	0
Ammospermophilus leucurus	0	0.01	0.01	0.01	0
Species richness	5	9	6	5	5
Abundance	18.32	8.01	2.66	6.22	11.36

TABLE C. Bird density (number per hectare), by habitat type, in Great Basin habitats of the Escalante Desert, Utah.

	Habitat type				
Species	Pinyon/ Juniper	Sagebrush	Grassland	Mixed shrub	Greasewood/ Shadscale
Accipiter cooperii	0.02	0	0	0	0
Zenaida macroura	0.20	0.03	3.18	0	0
Chordeiles minor	0	0	0	0	0.01
Aeronautus saxatalis	0	0.01	0	0	0
Colaptes auratus	0.02	0	0	0	0
Picoides villosus	0.04	0	0	0	0
Myiarchus cinerascens	0.14	0	0	0	0
Empidonax wrightii	0.02	0	0	0	0
Eremophila alpestris	0.29	0.01	5.63	0.79	0.52
Aphelocoma coerulescens	0.04	0	0	0	0
Gymnorhinus cyanocephalus	0.04	0	0	0	0
Parus inornatus	0.45	0	0	0	0
Psaltriparus minimus	0.18	0	0	0	0
Thyromanes bewickii	0.23	0	0	0	0
Mimus polyglottos	0.04	0	0	0	0
Oreoscoptes montanus	0.02	0	0	0.09	0.04
Sialia currucoides	0.02	0	0	0	0
Polioptila caerulea	0.02	0	0	0	0
Lanius ludovicianus	0.02	0	0	0.02	0.01
Vireo vicinior	0.02	0	0	0	0
Dendroica nigrescens	0.08	0	0	0	0
Sturnella neglecta	0	0	0.09	0	0
Carpodacus mexicanus	0.06	0	0	0	0
Loxia curvirostra	0.04	0	0	0	0
Pipilo erythrophthalmus	0.02	0	0	0	0
Chondestes grammacus	0.04	0	0	0	0
Amphispiza bilineata	0.78	0.05	0	0.11	0.05
A. belli	0	0.04	0	0.34	0.21
Spizella passerina	0.33	0	0	0	0
S. breweri	0	0	0	0.60	0.37
Unidentified	0.04	0.07	0.06	0	0
Species richness	25	6	3	6	7
Abundance	3.19	0.22	8.96	1.95	1.21